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Prevalence of tool behaviour is associated with pelage phenotype in intraspecific hybrid long-tailed macaques (*Macaca fascicularis aurea* × *M. f. fascicularis*)

Michael D. Gumert [a,b,h,*], **Amanda Wei Yi Tan** [c], **Lydia V. Luncz** [d], **Constance Ting Chua** [e,f], **Lars Kulik** [g], **Adam D. Switzer** [e,f], **Michael Haslam** [h], **Atsushi Iriki** [i,j] **and Suchinda Malaivijitnond** [b,k]

[a] Division of Psychology, School of Social Sciences, Nanyang Technological University, Singapore 639818, Singapore

[b] Department of Biology, Faculty of Science, Chulalongkorn University, Phayathai Road, Pathumwan, Bangkok 10330, Thailand

[c] Department of Anthropology, Durham University, Durham DH1 3LE, UK

[d] Primate Models for Behavioural Evolution Lab, Institute for Cognitive and Evolutionary Anthropology, University of Oxford, Oxford OX1 6PN, UK

[e] Earth Observatory of Singapore, Nanyang Technological University, Singapore 639798, Singapore

[f] The Asian School of the Environment, Nanyang Technological University, Singapore 639798, Singapore

[g] Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany

[h] School of Archaeology, University of Oxford, Oxford OX1 3QY, UK

[i] Laboratory for Symbolic Cognitive Development, RIKEN Center for Biosystems Dynamics Research, Kobe 650-0047, Japan

[j] Lee Kong Chian School of Medicine and RIKEN-NTU Research Centre for Human Biology, Nanyang Technological University, Singapore 636921, Singapore

[k] National Primate Research Center of Thailand, Chulalongkorn University, Saraburi 18110, Thailand

[*]Corresponding author's e-mail address: gumert@ntu.edu.sg

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Abstract
Stone-hammering behaviour customarily occurs in Burmese long-tailed macaques, *Macaca fascicularis aurea*, and in some Burmese-common longtail hybrids, *M. f. aurea* × *M. f. fascicularis*; however, it is not observed in common longtails. Facial pelage discriminates these subspecies, and hybrids express variable patterns. It was tested if stone hammering related to facial pelage in 48 hybrid longtails, across two phenotypes — hybrid-like ($N = 19$) and common-like ($N = 29$). In both phenotypes, tool users showed similar frequency and proficiency of stone hammering; however, common-like phenotypes showed significantly fewer tool users (42%) than hybrid-like phenotypes (76%). 111 Burmese longtails showed the highest prevalence of tool users (88%). Hybrid longtails living together in a shared social and ecological environment showed a significant difference in tool user prevalence based on facial pelage phenotype. This is consistent with inherited factors accounting for the difference, and thus could indicate Burmese longtails carry developmental biases for their tool behaviour.

Keywords
long-tailed macaque, tool behaviour, hybridization, phenotypic variation, developmental bias, learning, animal culture.

1. Introduction

Tool behaviour arises from varying combinations of ecological influences, social conditions, and underlying inherited tendencies, such as learning abilities and biases (Biro et al., 2013; Call, 2013; Hunt et al., 2013). Once innovated, tools can improve an animal's influence over its surroundings and increase their adaptive fit to the local environment (Biro et al., 2013). Tool behaviour yielding adaptive advantages would improve reproductive success, which in turn would drive a process of natural selection for the underlying dispositions and abilities supporting the behaviour. Developmental biases that could be selected for include directed perceptual and motivational systems towards relevant materials, tendencies to manipulate objects, associative learning abilities, social learning and cultural capacities, and other factors. Once directional selection is operating on the mechanisms underlying tool behaviour, the process of speciation could then be affected, establishing differences in tool-using abilities between closely-related taxa.

Identifying the degree to which inherited mechanisms contribute to any given tool behaviour has generated considerable debate since studies on animal tool behaviour began (van Lawick-Goodall, 1970; Beck, 1975; Bonner, 1980). The first complete theoretical focus on the matter considered the concept of cultural evolution through social learning, presenting the case that culture and genes affected the phenotype by two independent mechanisms of

evolutionary inheritance — cultural evolution and genetic evolution (Richerson & Boyd, 1978; Lumsden & Wilson, 1983; Boyd & Richerson, 1985, 1988). These two processes were modelled to compete for control of phenotypic traits, producing a gene-culture coevolutionary process, where for example, behavioural plasticity could be launched into culture from hypothetical genetic systems. This theoretical approach has since guided research on animal tool use and other forms of behaviour.

Although a very compelling approach, the culture-gene dichotomization has explanatory limits, and may not really be that fundamentally different from the classical nature vs. nurture debate, looking into environmentally or genetically-determined behaviour. This becomes evident when attempting to resolve which of the two evolutionary processes plays the larger role in explaining behavioural variation, as attempts to genuinely separate the two are usually stymied. For example, one large-scale genetic analyses in chimpanzees showed genetic correlations can account for geographical behavioural variation (Langergraber et al., 2011), while a similar analysis showed the contrary, supporting a cultural evolutionary account of the same behavioural variation (Lycett et al., 2009). Whether or not a culture vs. genetics debate, ever will, or could, be completely settled is not clear. What is certain, however, is that sociocultural processes exist and they extend from, interact with, and affect the underlying biology of animal behaviour (Whiten et al., 2017).

The animal cultures debate has continued (McGrew, 1998; Laland & Hoppitt, 2003; Krützen et al., 2006; Laland & Janik, 2006a,b), bringing together a more integrative outlook incorporating a variety of mechanisms for explaining cultural phenomenon that include environmental and genetic influences (Mesoudi et al., 2006; Laland et al., 2009). For example, there have been discussions of evolved social learning strategies (Laland, 2004) adaptive cultural transmission biases (Price et al., 2017), and ecological inheritance through niche construction (Laland et al., 2000; Odling-Smee et al., 2003). These ideas connect into a new conceptual framework, called the extended evolutionary synthesis, which discusses mechanisms that generate phenotypic plasticity during development and how such changes can feedback into the species' evolution (Laland et al., 2015). This approach builds from the past population genetic models of inheritance, to more interdependent models on the role that environment and inherited factors have, including genes

and cultural constructs, in the adaptation of behavioural traits to local conditions.

In regards to animal tool behaviour, a better understanding is needed of how the social and ecological environments interact with inherited predispositions and abilities. Socially-produced cultural constructs and information can be an important part of an individual's evolutionary environment, which can select for inherited dispositions and evolved cognitive mechanisms that direct an organisms attention to these relevant aspects of their environment (Lotem et al., 2017). From this, inherited biases affecting tool behaviour are expected to be observable. First, there can be a niche construction of relevant materials and remains of past-used artefacts, as well as associated developmental biases for directing attention and preferences to these materials (Fragaszy et al., 2013). Second, there can be suitable social settings, such as more tolerance during interaction (van Schaik, 2003), along with biases for individuals to attend to their conspecifics and their relevant actions (Laland, 2004; Fragaszy et al., 2017; Tan et al., 2018). The main point here being that sociocultural elements of the environment should interact with internal developmental biases. To uncover how such biases integrate into tool behaviour development, novel methodological approaches will have to be carried out (Laland & Janik, 2006a). Paradigms are needed that allow the study of how social factors, ecological conditions, and individual-level traits contribute collectively to adaptive behaviour.

1.1. Hybrid studies: a new approach to tool behaviour

Studies of hybridized tool-using animals present a novel approach for disentangling inherited biases from environmental influences by offering greater control over the shared environment of different types of individuals. Hybrid zones are common in nature and are areas where different species or subspecies converge and form hybridized offspring, often resulting in variable and intermediate phenotypes (Zinner et al., 2011). Hewitt (1988) considered hybrid zones "natural laboratories" for discriminating the degree of genetic and non-genetic contributions to behaviour. For example, biologically-based dispositions for social behaviour have been discovered using hybrid studies, and the research programs discovering them began by associating parent-type morphological indicators with behavioural variation in field settings (Nagel, 1973; Sugawara, 1979, 1988; Bergman & Beehner, 2004; Bergman et al., 2008; Kelaita & Cortés-Ortiz, 2013).

These hybrid studies on social behaviour provided compelling results regarding inherited behavioural dispositions related to social structure. Studies on intraspecific hybrids of hamadryas and olive baboons (*Papio hamadryas hamadryas* × *P. h. anubis*) and interspecific hybrids of howler monkeys (*Alouatta pigra* × *A. palliata*) have both shown inherited links to their social behaviour. In the baboon case, hybrids showed dispositions towards the socio-sexual behaviour characteristic of the parent subspecies they most resembled (Sugawara, 1979, 1988; Bergman & Beehner, 2004; Bergman et al., 2008). Similarly, in howler monkeys, *A. pigra*-like hybrid females showed social behaviour truer to the parent type they most resembled (Kelaita & Cortés-Ortiz, 2013; Ho et al., 2014; Cortés-Ortiz et al., 2015). These correlations between morphological features and social behaviour, cued the researchers to the possibility that inherited factors were contributing to behavioural features adapted to their social systems. Their subsequent research later found partial associations with genetic fingerprinting, supporting that the observed connection between morphological phenotype and socially-adapted behaviour likely resulted from genetic-based inherited dispositions (Bergman et al., 2008; Ho et al., 2014).

The hybrid approach clearly was able to show that inherited biases can play an integrative role in the development of social structuring through individual-level social predispositions in monkeys. This method appears useful to examining tool behaviour as well, as it could potentially reveal similar inherited developmental biases for tool behaviour. Towards this aim, after recognizing individual variation in a key subspecies-discriminating morphological marker at one of our sites, our team launched a behavioural study on stone-hammering behaviour in an intraspecific hybrid population of long-tailed macaques at Khao Sam Roi Yot National Park, Thailand.

1.2. Long-tailed macaque stone tool behaviour

Stone-hammering behaviour can occur in hybrid long-tailed macaques that are a natural cross between the Burmese (*Macaca fascicularis aurea*) and common (*M. f. fascicularis*) subspecies (*M. f. aurea* × *M. f. fascicularis* hybrids are hereafter referred to as hybrid longtails). The two parent subspecies, however, differ considerably in their tool behaviour, and also in their pelage features, providing an opportunity for a natural test of the relationship between tool behaviour and morphological phenotype in hybrids. Regarding tool use, Burmese longtails are regular tool users, while common longtails

rarely use tools. Burmese longtails use stones as hammers to open marine prey and seeds in rocky areas around coasts across the Andaman Sea region of southern Thailand and southern Myanmar (Carpenter, 1887; Malaivijitnond et al., 2007; Gumert & Malaivijitnond, 2012). In contrast, common longtails are not prevalent tool users, and they do not frequently use stone tools in wild conditions, if at all. Hybrid longtails, on the other hand, do sometimes exhibit regular stone-hammering behaviour similar to Burmese longtails, but little is really known about variation in their tool behaviour (Bunlungsup et al., 2016).

The difference in stone-hammering behaviour between the two subspecies appears real. Laboratory tests and field observations support this conclusion. First, a lab study rigorously attempted to train common longtails in stone-hammering behaviour and failed (Bandini & Tennie, 2018); however, common longtails have some limited tool abilities, as they have spontaneously learned how to use stick tools in captivity (Zuberbühler et al., 1996). Second, in highly human-influenced settings, with an abundance of accessible anthropogenic foods and objects (e.g., temples), isolated bouts of stone pounding are occasionally reported. These few cases are part of an array of non-functional play with stones, otherwise known as stone handling (Wheatley, 1988, 1999; Fuentes et al., 2005; Pelletier et al., 2017). Such stone pounding, however, has never developed into regular stone use for foraging, despite the obvious opportunity for it.

Further supporting the difference in tool behaviour, common longtails have been studied in numerous places and are one of the easiest primates to observe in Southeast Asia, yet they have never been observed using tools like Burmese longtails. The absence of finding any regular stone-hammering behaviour anywhere in their range, therefore, is quite noteworthy. Fooden (1995) travelled through most of the long-tailed macaque range collecting pelage specimens and noted the tool use in Myanmar, but he did not report stone-hammering behaviour anywhere else. Other efforts have been carried out to find tool behaviour throughout Thailand and Myanmar, but have failed to uncover cases of stone-hammering behaviour in any common longtails (Gumert et al., 2014, 2016). Furthermore, past nationwide macaque surveys have been conducted throughout Thailand, and these also have not indicated any examples of stone-hammering behaviour in common longtails (Malaivijitnond et al., 2005; Malaivijitnond & Hamada, 2008).

The absence of stone hammering in common longtails cannot be fully accounted for by the two subspecies inhabiting different environments. Surveys of common longtails have been conducted in the very same habitats in which Burmese longtails use stone tools, such as mangroves and rocky shores; and with the same prey available, such as hooded rock oysters (*Saccostrea cucullata*), nerite snails (*Nerita* spp), trochid snails (e.g., *Monodonta labio*), muricid snails (e.g. *Thais* spp and *Morula* spp) and sea almonds (*Terminalia catappa*). At these sites, however, common longtails do not use stone hammers, or even eat molluscs. In contrast, Burmese long-tailed macaques reliably and frequently use tools in such coastal environments, and the behaviour constitutes, on average, 41% of their activity when foraging in those habitats (Gumert et al., 2019). It must also be considered that tool remains are very easy to find at Burmese longtail coastal sites (Gumert et al., 2009; Haslam et al., 2013; Falótico et al., 2017), yet are never found where common longtails inhabit coasts.

Weighing the available evidence, Burmese macaque stone hammering happens in very high prevalence, ordinarily occurs in undisturbed environments, and can be negatively influenced by human activity (Gumert et al., 2013). Common longtails seem only to touch and manipulate stones in human disturbed areas, and never exhibit any regular stone tool use like Burmese longtails do. It is therefore justifiable to predict a strong linkage between a tool-based mollusc predation strategy and the Burmese subspecies, based on the hypothesis that Burmese longtails have associated capacities that have evolved in tandem with their past ecological and social conditions. Observing a connection between stone-hammering behaviour and Burmese pelage features in hybrid longtails would be consistent with this hypothesis.

Throughout south and central Thailand, hybrid longtails inhabit an intraspecific hybrid zone where the Burmese and common longtail ranges overlap (Figure 1). This range is based on the study of pelage samples referred to above (Fooden, 1995). Fooden showed the key difference between his Burmese and common longtail pelage samples was a distinct variation in their facial pelage. Other than this marker, morphological differences amongst long-tailed macaque subspecies have been found to be minor and less distinct (Fooden, 1995; Bunlungsup et al., 2016). Consequently, at this point, facial pelage variation is the primary key marker known for discriminating the two subspecies. Where the subspecies hybridize, there is an admixture of facial pelage pattern that ranges in variation between the parent types. That is, some individuals look more Burmese-like than others.

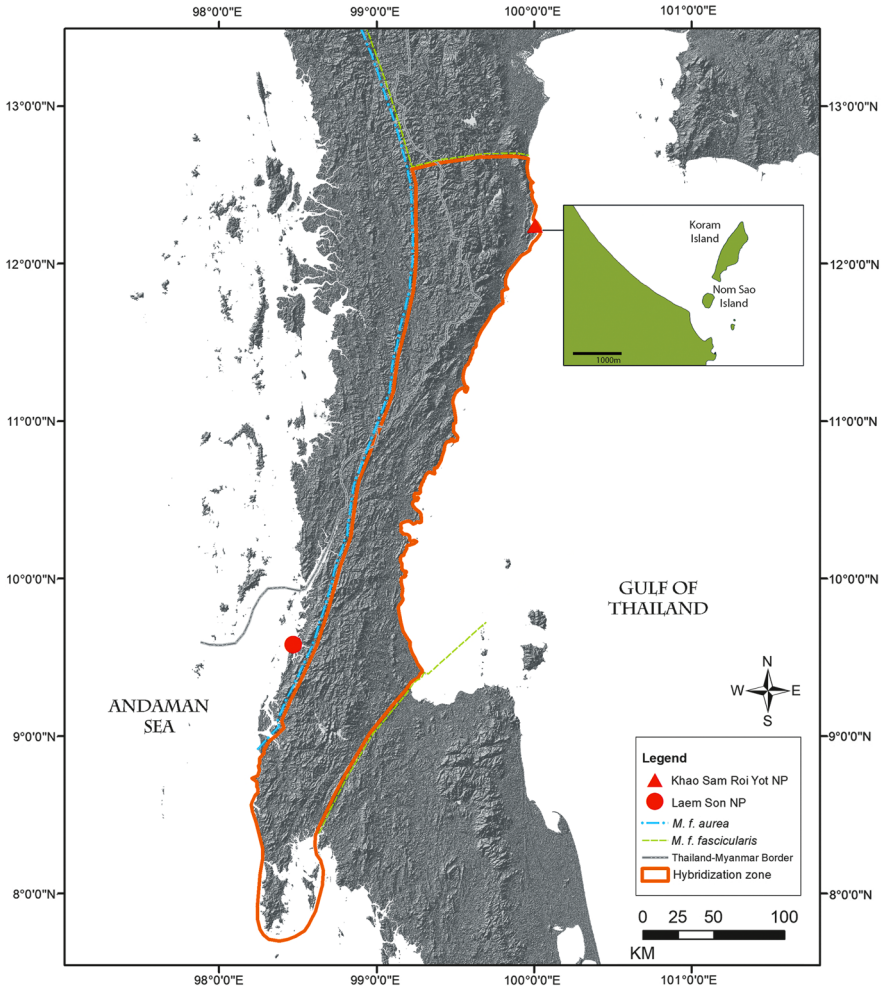


Figure 1. A map of the long-tailed macaque range in southern Thailand and Myanmar, showing the zone where Burmese and common longtails hybridize around the Tenasserim Hills in southern Thailand. Data were used from macaques at two parks in Thailand, Laem Son National Park and Khao Sam Roi Yot National Park, both marked on the map. Burmese longtails inhabited Laem Son, and hybrid longtails inhabited Khao Sam Roi Yot. The hybrid longtail phenotype study was conducted on macaques from Koram and Nom Sao Islands, shown in the inlay.

1.3. A study of hybrid longtail tool behaviour

The facial pelage variation found in hybrid longtails provides an opportunity to test for Burmese-associated biases in macaque stone-hammering

behaviour. Since these pelage patterns are distinctively different between the two subspecies, the elements in an individual's pelage pattern are partially indicative of their pedigree. It should therefore be expected that if tool behaviour is also associated to a Burmese longtail pedigree and supported by inherited mechanisms from that line of descent, then facial pelage features and tool-use behaviour should be statistically correlated in hybrids. If on the other hand, stone hammering is not associated with mechanisms associated to a Burmese inheritance, but rather develops from similar abilities across the entire long-tailed macaque species, then it would be expected that hybrid longtails living together in a shared environment should all develop a similar form and prevalence of stone-hammering behaviour. This scenario would be reflected in finding no statistical associations between an individual's tool behaviour and parent-type facial pelage patterns.

Ignoring the above reported findings, the null hypothesis would be that long-tailed macaque stone-hammering behaviour develops from a general mechanism, or array of mechanisms, shared across the entire species. The shared mechanism could be a few things. First, it could be an associative learning ability shared across the species that equally biases the likelihood of stone-hammering development across all individuals when in habitats containing rocks and encased foods. Another possibility is a non-specific social learning ability allowing any hybrid individual to acquire tool-use behaviour, as long as there are observable individuals in their social group performing the behaviour near them. Another general social-based learning mechanism could be associated to niche construction. That is, having available used artefacts to learn from around them, but to remain non-specific this would require there be an equal interest in these artefacts between subspecies type. Asocial and social learning abilities are not mutually exclusive, and it could also be a mixture of these mechanisms. It could even be the result of other mechanisms affecting the learning of tool behaviour, such as a directed interest in object manipulation, preference for mollusc consumption, sensory and motivational biases for handling the materials, an adequate motor capacity, a tolerant social disposition, etc. That the mechanisms in operation cannot be clarified in this study is not our major concern here. What is important to this null hypothesis; however, is that whatever array of mechanisms might be operating, all long-tailed macaques are similarly affected and it is regardless of subspecies type.

The alternative hypothesis to the above scenario was based on current evidence. There is no indication that common longtails and Burmese longtails share the same abilities for acquiring stone-hammering behaviour. This leads to the hypothesis that the Burmese subspecies has a stronger, more directed capacity for stone-hammering behaviour and would more reliably acquire stone hammering when their development occurs in the appropriate social and ecological context than other varieties of macaque. This could be owing to Burmese longtails inheriting developmental biases associated to any, or all, of the above discussed mechanisms.

A field study was designed to examine this matter in hybrid longtails, on which our team was already conducting observational studies. If stone-hammering behaviour is developed and learned through general mechanisms found across the entire long-tailed macaque species, regardless of subspecies variety, it would be predicted that there is no correlation between a morphological subspecies marker and tool behaviour in hybrid longtails developing in a shared environment. This is because all these individuals presumably share relatively similar capacities and would be affected by the same general social and ecological conditions. Thus, without any variation in internal biases across individuals, it would be unlikely that any set of individuals should have a notable advantage over others for developing and performing tool behaviour. In contrast, if the alternative hypothesis is true, then finding an association between stone-hammering behaviour and the Burmese facial pelage pattern would be indicative of a common descent of tool behaviour with other Burmese inherited features. Such a finding would be consistent with the existence of subspecies-linked developmental biases for stone-hammering behaviour.

In this study, four tests were run to explore for statistical associations between facial pelage and stone-hammering behaviour in hybrid longtails. Behavioural data were used from two groups of habituated hybrid longtails living on Koram and Nom Sao Islands in Khao Sam Roi Yot National Park (Tan et al., 2016, 2018; Luncz et al., 2017b; Tan, 2017). Each hybrid longtail subject was categorized by their facial hair pelage pattern into differing phenotypes. Three tests were run to compare different aspects of tool behaviour between phenotypes. The first test compared tool user prevalence between phenotypes and also ran a comparison with an outgroup of pure Burmese longtails at Laem Son National Park. The second test compared how often each phenotype used tools, and a third test compared the proficiency of each

phenotype in stone hammering. In a fourth test, it was considered whether tool users showed any bias in social closeness to phenotypes that were relatively more Burmese-like. This was done to show if phenotypic differences in tool behaviour could be explained by a commonly shared non-specific social learning mechanism from whoever one associates. Results were then evaluated for a relationship between stone-hammering behaviour and the Burmese subspecies.

2. Methods

2.1. Study sites and subjects

This study was on long-tailed macaques from two national parks in Thailand (Figure 1). First, a population of hybrid longtails (*M. f. fascicularis* × *M. f. aurea*) was sampled from Koram and Nom Sao Islands in Khao Sam Roi Yot National Park, located in Prachuap Khiri Khan Province along the Gulf of Thailand. Here, hybrid longtails were found on the mainland, Koram Island and Nom Sao Island. The group on Nom Sao Island was not a separate population from Koram, as these males have emigrated off of Koram Island, about 400 m away (Tan et al., 2016). At the second site, a population of Burmese longtails (*M. f. aurea*) was sampled from Piak Nam Yai Island in Laem Son National Park located in Ranong Province along the Andaman Sea. Here, tool-using Burmese longtails inhabited the mainland, Piak Nam Yai Island, and Thao Island. The features of these studies sites, macaque populations, and data collection have already been reported for Piak Nam Yai (Gumert et al., 2013), Koram (Tan, 2017; Tan et al., 2018) and Nom Sao (Tan et al., 2016; Luncz et al., 2017b).

2.2. Data collection

No behavioural data were collected specifically for this study, as the possibility for this test was recognized after already running other projects. Most of the data for this study was drawn out of a behavioural data set on 72 habituated hybrid longtails on Koram Island in Khao Sam Roi Yot collected by AT between 17 October 2013 and 2 December 2014 (Tan, 2017; Tan et al., 2018). From the Koram group, a sample of 39 mature macaques was used (i.e., adults and adolescents), of which 38 were studied during the above focal sampling, which totalled 256 h 16 min across these subjects. Also, 7039 sampled tool-use bouts were used from the subjects that were tool users. One

of the 39 subjects was a male that emigrated into the Koram group after the above mentioned year of focal sampling was completed. He was observed and assessed for tool use during the next study, in 2015, discussed below.

Other data for this study was drawn from two other sites. First, data were used from a behavioural sample collected on a nearby group of nine habituated adult male hybrid longtails at Nom Sao Island, during a study by AT and LL on Koram and Nom Sao between 20 September to 24 October 2015 (Tan et al., 2016; Luncz et al., 2017b). During this time, food test experiments were run on Nom Sao and Koram, providing the subjects with tool opportunities. The nine new subjects on Nom Sao were observed for approximately 65 h, during which all were observed in foraging contexts and exposed to tool-use opportunities. On Koram, the one new male subject was observed across several days, in multiple foraging contexts, and around experimental tests. Ad lib notes indicated he never used tools and only showed scrounging behaviour of molluscs, a behaviour highly characteristic of non-tool users. Second, data were used out of a sample collected from a population of 192 unhabituated Burmese longtails on Piak Nam Yai Island in Laem Son National Park. The island was visited by MG for 91 days between 15 January to 24 June 2011, and macaques were directly observed by boat for 167 h 56 min (Gumert et al., 2013). From these observations, 111 mature individuals, from nine different groups, were assessed for tool user prevalence, using 3272 scan samples, adlib notes on tool behaviour, and 15 h of focal sampling collected during the study.

2.3. Assessment of facial hair pattern

During the behavioural studies at Koram, it was recognized that individuals could be discriminated as more or less Burmese-like by facial pelage pattern, based on Fooden's (1995) descriptions. These differences in facial pelage amongst the macaques on Koram and Nom Sao Islands were studied, categorized, and then compared with stone-hammering behaviour. Side-of-face photographs were taken of the macaques by AT, profiling all individuals that could be clearly photographed. After reviewing the photographs, only mature individuals could be reliably discriminated ($N = 48$). On Koram Island, most adult and adolescent individuals were adequately photographed ($N = 39$), but not all were due to conditions in the field. On Nom Sao Island, all the macaques were photographed ($N = 9$). The photographs from the 48 individuals were used to assign a phenotype to each subject based on their

preauricular hair and lateral crest pattern (Figure 2). AT and MG each independently assessed the photographs based on the distinctive facial pelage patterns of Burmese and common longtails, which allowed a reliability comparison. A more complete justification for use of this morphological marker is reviewed below in the Discussion.

Burmese and common longtails have distinctly different facial pelage patterns (Fooden, 1995). The Burmese longtail facial pelage pattern has posterior and ventral-directed preauricular hair and an infrazygomatic lateral crest (Figure 2a). The common longtail facial pelage pattern has anterior and dorsal-directed preauricular hair and a transzygomatic lateral crest (Figure 2d). Intermediate phenotypes amongst hybrid longtails have mixed elements of both types (Figure 2b) and can sometimes exhibit lateral crest whorls, another feature found in Burmese, but not common longtails (Figure 3). The preauricular hair was scored for whether it was directed posteriorly, anteriorly, ventrally, dorsally, or in combination of these patterns. The lateral crest was then scored for being transzygomatic, infrazygomatic,

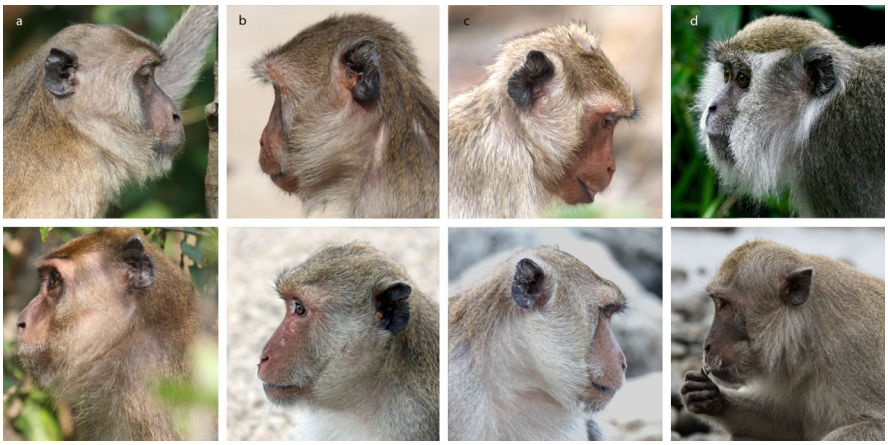


Figure 2. The facial pelage pattern varies between Burmese and common longtails. These patterns are presented in photographs of Burmese longtails (a), two phenotypes of hybrid longtails, hybrid-like pattern (HY) (b) and common-like pattern (CM) (c), and common longtails (d). Pre-auricular hair is smooth and directed posteriorly in Burmese longtails, while in common longtails it is directly anteriorly. The lateral crest in Burmese longtails run horizontal across the face (infrazygomatic), but runs vertically across the face in common longtails (transzygomatic). Hybrid longtails show mixtures of these patterns. Females are shown on top row and males on bottom. Photograph credits: (a) Michael D. Gumert; (b), (c) Amanda Wei Yi Tan; (d♀) Michael D. Gumert; (d♂) Jean-Baptiste Leca.

Figure 3. Example of a lateral crest forming a whorl pattern.

diagonal, whorled, or any combination of these. A phenotype was then assigned, depending on the subject's matching or mixing with either of the parent-types described above. In the study, two phenotypes were observed, hybrid-like (HY) and common-like (CM). The HY phenotype was more like the Burmese longtail pattern than the CM phenotype, and CM was hard to discriminate from the common longtail pattern.

2.4. Test 1: tool user prevalence in hybrid and Burmese longtails

Test 1 compared whether the number of tool users varied across the three samples, which included (1) the hybrid-like phenotype (HY, $N = 29$), (2) the common-like phenotype (CM, $N = 19$), from the hybrid longtails at Khao Sam Roi Yot and (3) the pure Burmese longtails from Laem Son (BM, $N = 111$). Subjects that were never observed to use a tool in any observations or experiments were categorized as non-tool users, which was possible to do accurately because macaque tool use is not difficult to observe. Burmese longtails and their hybrids use stone hammers frequently on shores. Around 40% of the coastal foraging activity in Burmese longtails involves holding or using a stone hammer (Gumert et al., 2019), while in hybrid longtails tool-use behaviour occurs in around 20% of their total time focal sampled (Tan, 2017). Another study showed that up to 76% of scan samples can involve

tool use in female macaques in feeding contexts on the coast (Gumert et al., 2011), while in only 11 h of another study, thousands of tool-use bouts were observed in a single group (Haslam et al., 2016).

Test 1 was done using a generalized linear mixed model (GLMM) with binomial error structure and logit link function (Baayen, 2008). In the dataset, each individual comprised one data point ($N = 159$). The response variable was set to tool user status — tool user or non-tool user. The fixed effect in this model was the three samples — Burmese longtail, BM, and hybrid longtails, HY and CM. Sex and age (i.e., adolescent or adult) were added as control variables to account for any effects these factors had on tool behaviour. They were not interpreted (Mundry, 2014). For random effects, two factors were included, geographical location (i.e., Andaman Sea or Thai Gulf coasts) and social group (9 for Burmese longtails and 2 for hybrid longtails = 11 possible social groups), and these factors accounted for the localized social and ecological differences. To keep type I error rates at 5% (Barr et al., 2013), all possible random slopes were included, which was for sex and age within location and group.

2.5. Tests 2 and 3: hybrid effects on performance of tool behaviour and skill

Test 2 and Test 3 compared whether performance of stone-hammering behaviour and its skill, or proficiency, differed between the hybrid longtail phenotypes, HY and CM, in the Koram group. All the hybrid longtail tool users on Koram Island from Test 1 were used ($N = 26$), as the Koram group's focal sample dataset provided adequate measures for such an analysis. Here, differences in tool behaviour between the HY and CM phenotypes were compared in two models, Test 2, time engaged in tool use during foraging, and Test 3, proportion of successful tool-use bouts. For Test 2, the proportion of time engaged in tool use during foraging was assessed in 26 subjects, while for Test 3, the proportion of tool-use bouts successful in opening food was assessed in 25 subjects. These samples had fewer subjects than the entire Koram group sample in Test 1 ($N = 39$) because variation in tool behaviour could only be tested in hybrid longtail tool users ($N = 26$ tool users, $N = 13$ non-tool users). Furthermore, Test 3, the tool-bout success analysis, had one fewer subject. This was because the individual disappeared early in the study and did not have enough tool bout samples to compare with others for success. It was possible, however, to calculate time spent in tool behaviour during that subject's focal samples.

For both tests, GLMM's with binomial error structure and logit link function were used. For Test 2, the proportion of time engaged in tool behaviour during total time foraging was analysed. In R, such an analysis of proportional data is possible by using a two-column matrix. One column was the proportion of time engaged in tool behaviour while foraging, and the response column was proportion of time during foraging not engaged in tool behaviour. The two hybrid longtail phenotypes, HY and CM, were included as the fixed effect and sex, age, coastal environment and tidal levels were entered as uninterpreted control variables. Coastal environments were entered as rocky shore and sandy beach, and tides were categorized as low, middle, or high. Two random effects were entered. The first was individual identity, and the second random factor was a pseudo-replication control that comprised as many levels as data points. This second random factor was used because the response variable, proportion of time in tool use, was entered as a two-column matrix to account for the measure being a proportion, as described above. In Test 3, the number of successful or failed tool-use bouts were entered as the response variable. Phenotype was set as the fixed effect, HY or CM. Sex and age were set as control variables and individual identity was included as a random effect.

2.6. Test 4: social proximity and phenotypic variation in tool use

After results from Tests 1–3 were assessed, Test 4 was run to test if non-specific social learning could account for the results. Test 4 used 38 of the 39 animals from the Koram Island group that were used in Test 1. Here, social proximity (i.e., time within 1 m) was added into the model as a measure of social association with HY individuals. This assessed whether the data were more consistent with stone-hammering behaviour being acquired through an unbiased mechanism associated to social closeness found across all the subjects, or if the results remained consistent with a phenotypic difference in tool behaviour between the HY and CM phenotypes. In Test 4, one non-tool user subject was missing because this male was first observed after the Koram group focal samples were already collected. This subject was not focal sampled and thus unable to be used for any other testing, except Test 1.

To run Test 4, there was no need for any random factors in this model because each subject only had one data point, hence, a generalized linear model (GLM) with binomial error structure and logit link function was used (McCullagh & Nelder, 1989). A composite measure of each subjects' proportion of time in proximity to all HY individuals was included, measured

as the proportion of time the subject was in proximity to any HY macaque during their focal samples. This measures is considered an appropriate proxy of overall social association and relationship quality (van Schaik & Aureli, 2000). The two phenotypes, HY and CM, were the fixed effect. Sex and age were put in as uninterpreted control variables. Prior to running the model, the proximity rate was z-transformed to a mean of zero and a standard deviation of one.

2.7. Statistical validations

Consistency within the models was checked and assessed for overall significance of the predictors. Each model was checked for model stability. To do this, levels of the random effects were excluded from the data one at a time to derive model estimates in these conditions. Each derived model estimate was then compared with the model estimates of the full data set. These checks indicated no influential cases to exist. Variance inflation factors (VIF) (Quinn & Keough, 2002) were derived using the function vif of the R-package car (Fox & Weisberg, 2011) and this check did not indicate collinearity to be an issue. For the GLM, model diagnostics were run using the R functions "dfbeta" and did not indicate any assumptions to be violated. To determine the overall significance of the predictors, a likelihood ratio test was used (Dobson, 2002) (LRT; R function 'anova', package 'stats'). This compared the fit of the full model with a null model lacking the fixed effects (Forstmeier & Schielzeth, 2011). The P-values for the fixed effects were also based on a LRT, comparing the full model with a model reduced by the fixed effect (Dobson, 2002; Barr et al., 2013) using the function 'drop1' from the 'stats' package. The GLMM's were fitted using the function glmer of the R package lme4 (Bates et al., 2015), and the GLM using the function glm from the 'stats' package. All models were implemented in R (2016) and analyses run by LK.

2.8. Map development

A map was drawn of the estimated range of Burmese, common, and hybrid longtails, based on pelages found and examined by Fooden (1995) and surveys in Thailand and Myanmar (Malaivijitnond et al., 2005; Malaivijitnond & Hamada, 2008; San & Hamada, 2011; Gumert et al., 2014, 2016). A relief map was developed from 90 m resolution Digital Elevation Models (DEM) from NASA Shuttle Radar Topographic Mission (SRTM). Hill-shading tools

were used to portray the shaded relief, with azimuth and altitude set at 315° and 45°, respectively. Bilinear interpolation was then applied to the map to smooth it. The locations of both study sites were also added. The map was drawn by CC and AS using ArcGIS 10.2.2.

3. Results

3.1. Facial pelage typing

Assessment of facial hair pelage in the hybrid longtails at Khao Sam Roi Yot revealed two types: (1) a hybrid-like pattern (HY) (Figure 2b), which showed mixed features of the parent types and (2) a common-like pattern (CM) (Figure 2c), which closely matched the common longtail parent type. In total, there were 19 CM (40%) and 29 HY (60%) phenotypes categorized for this analysis (Koram: HY = 23, CM = 16; Nom Sao: HY = 6, CM = 3). CM subjects showed anterior and dorsal-directed preauricular hair and a transzygomatic lateral crest pattern typical of *M. f. fascicularis*. The HY phenotype was more similar to the Burmese longtail pattern than the CM phenotype. HY subjects showed an incomplete mixture of each subspecies traits and showed observable elements of the Burmese longtail facial pelage pattern. In HY, the preauricular facial pelage contained elements of posterior and ventral-directed preauricular hair and also showed mixed elements of both trans and infrazygomatic cheek crests (Figure 2b top), crests running diagonally across the cheek (Figure 2b bottom), or whorls (Figure 3). There were no hybrid longtail subjects completely expressing a Burmese longtail pelage pattern, although some were quite close. Both AT and MG's assessments of phenotype of the hybrid longtails matched without disagreement. No pelage analysis was done on the BM sample ($N = 111$) from Laem Son. This sample occurred in the Burmese longtail range (Figure 1) and all express the Burmese pelage pattern (Figure 2a).

3.2. Test 1: tool user prevalence

In Test 1, the number of tool users across the three test samples (BM, HY, CM) were compared (Table 1) and a significant difference was found between them (GLMM Group LRT: $\chi^2 = 12.295$, df = 2, $p = 0.002$) (Figure 4). In the pure Burmese longtail sample (BM), 98 of the 111 subjects (88%) were tool users, while in the hybrid longtails (HY and CM), 30 of the 48 subjects (63%) were tool users. Amongst the hybrid longtails, there was a

Table 1.
Prevalence of tool users across samples.

		BM		HY		CM	
		Tool	*n*	Tool	*n*	Tool	*n*
Adult	♀	46 (85%)	54	9 (69%)	13	2 (40%)	5
	♂	23 (88%)	26	8 (73%)	11	4 (40%)	10
Adolescent	♀	11 (92%)	12	1 (100%)	1	0 (0%)	1
	♂	18 (95%)	19	4 (100%)	4	2 (67%)	3
Total		98 (88%)	111	22 (76%)	29	8 (42%)	19

Tool, number of tool users; *n*, total number of individuals in the sample; BM, a sample of pure Burmese longtails on Piak Nam Yai Island; HY, a sample of hybrid-like phenotypes from hybrid longtails on Koram and Nom Sao Islands; CM, a sample of common-like phenotypes from hybrid longtails on Koram and Nom Sao Islands.

significant difference between the two phenotypes in tool user prevalence. In HY, 22 of the 29 subjects were tool users (76%), while only 8 of the 19 subjects in the CM phenotype were (42%). The higher prevalence of tool users in the HY sample was statistically significant ($E_{CM\ vs.\ HY} = -1.739$, SD = 0.677, $\chi^2 = 6.575$, df = 1, $p = 0.010$). The CM sample was found to also

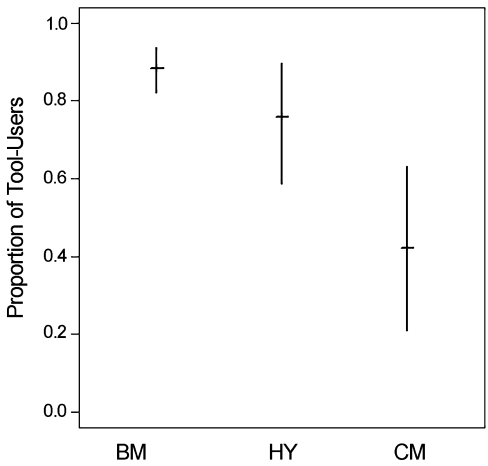


Figure 4. The prevalence of tool users varied across three samples in Test 1 (Burmese longtails: BM, hybrid longtails: HY, CM). CM had a significantly smaller proportion of tool users than both BM and HY. HY and BM did not significantly differ. Y-axis shows the proportion of tool users in each sample. Bars represent 95% confidence intervals.

Table 2.
Test 1: Differences in tool user prevalence across three samples, Burmese longtails (BM) and hybrid longtails (HY, CM) (full vs null $\chi^2 = 14.898$, $n = 159$, df $= 4$, $P = 0.005$).

	Estimate	SE	df	χ^2	*P*
(Intercept)	1.735	0.345	a	a	a
Tool user prevalence, BM, HY, CM	–	–	2	12.295	0.002
Tool user prevalence, BM, HY	−0.870	0.557	1	2.304	0.129
Tool user prevalence, BM, CM	−2.609	0.630	1	7.409	0.006
Tool user prevalence, HY, CM	−1.739	0.677	1	6.575	0.010
Age (adolescent)[b]	0.829	0.633	1	1.881	0.170
Sex (male)	0.382	0.510	1	0.574	0.449

[a] Not shown because does not have meaningful interpretation.
[b] Ages used were adolescent and adult, both of mature tool-user age.

have significantly fewer tool users than the pure Burmese longtail sample (BM) ($E_{BM\ vs.\ CM} = -2.609$, SD $= 0.630$, $\chi^2 = 7.409$, df $= 1$, $p = 0.006$). The HY sample, however, did not significantly differ from the BM sample ($E_{BM\ vs.\ HY} = -0.870$, SD $= 0.557$, $\chi^2 = 2.304$, df $= 1$, $p = 0.129$) (Table 1 and 2).

3.3. Tests 2 and 3: tool-use characteristics

Taking all the tool-using hybrid longtail subjects from the Koram Island group used in Test 1, Test 2 was run to compare differences across phenotype for time engaged in tool behaviour ($N = 26$) (Table 3). Test 3 was run to compare across phenotypes in their success at opening foods during tool-use bouts ($N = 25$) (Table 4). This analysis revealed no significant difference in the tool users of either phenotype sample (Figure 5). HY and CM tool users could not be shown to significantly differ in the proportion of time they engaged in stone hammering during foraging ($N = 26$, $E_{CM\ vs.\ HY} = -0.214$, SD $= 0.328$, $\chi^2 = 0.382$, df $= 1$, $p = 0.536$) (Figure 4), nor in how successfully they opened food with tools ($N = 25$, $E_{CM\ vs.\ HY} = -0.175$, SD $= 0.177$, $\chi^2 = 0.977$, df $= 1$, $p = 0.323$) (Figure 4). Tests 2 and 3 yielded no significant differences between the HY and CM phenotype samples in these two characteristics of stone-hammering behaviour.

3.4. Test 4: social closeness and tool user prevalence

In Test 4, social proximity was used to assess whether social closeness could have affected the tool user prevalence result from Test 1 through a non-specific social learning mechanism shared by both phenotypes. Here, social

Table 3.
Test 2: Differences between the two hybrid longtail phenotypes (HY, CM) in time engaged in tool use, measured by proportion of time using tools during time spent foraging (full vs null $\chi^2 = 151.740$, $n = 26$, df $= 6$, $P < 0.001$).

	Estimate	SE	df	χ^2	*P*
(Intercept)	−9.746	0.556	[a]	[a]	[a]
Time in tool use, HY and CM	−0.214	0.328	1	0.382	0.536
Age (adolescent)[b]	0.917	0.356	1	4.822	0.028
Sex (male)	−0.524	0.329	1	1.770	0.183
Environment (rocky shore)[c]	2.992	0.339	1	58.444	<0.001
Tidal level (Low)[d]	4.205	0.398	2	106.850	<0.001
Tidal level (Mid)[d]	3.381	0.408			

Tidal level and environment type strongly influenced tool use, occurring most during low tide on rocky shores. Adolescents spent more time on tool use.

[a] Not shown because does not have meaningful interpretation.

[b] Ages used were adolescent and adult, both of mature tool user age.

[c] Environments were rocky shore or sandy beach.

[d] Tidal levels were low (<33% covered), middle, and high (>67% covered) tidal levels.

proximity to HY macaques was added in as another predictor in the tool user prevalence analysis done in Test 1, but only amongst the macaques from the Koram Island group, minus one subject ($N = 38$) (see Methods). In the HY sample, 19 of the 23 subjects used tools (83%), while in the CM sample, 7 of the 15 subjects were tool users (47%). The results of Test 4 demonstrated that the association between prevalence of tool users and facial pelage pattern was still highly significantly associated ($E_{HY\ vs\ CM} =$

Table 4.
Test 3: Differences between the two hybrid longtail phenotypes (HY, CM) in proficiency of tool use, measured by proportion of successful tool-use bouts out of all bouts (full vs null $\chi^2 = 7.12$, $n = 25$, df $= 3$, $P = 0.0068$).

	Estimate	SE	df	χ^2	*P*
(Intercept)	2.186	0.179	[a]	[a]	[a]
Successful tool bouts, HY and CM	−0.175	0.177	1	0.977	0.323
Sex (male)	0.109	0.178	1	0.375	0.540
Age (adolescent)[b]	−0.477	0.190	1	5.633	0.018

Adults were more proficient than adolescents.

[a] Not shown because does not have meaningful interpretation.

[b] Ages used were adolescent and adult, both of mature tool user age.

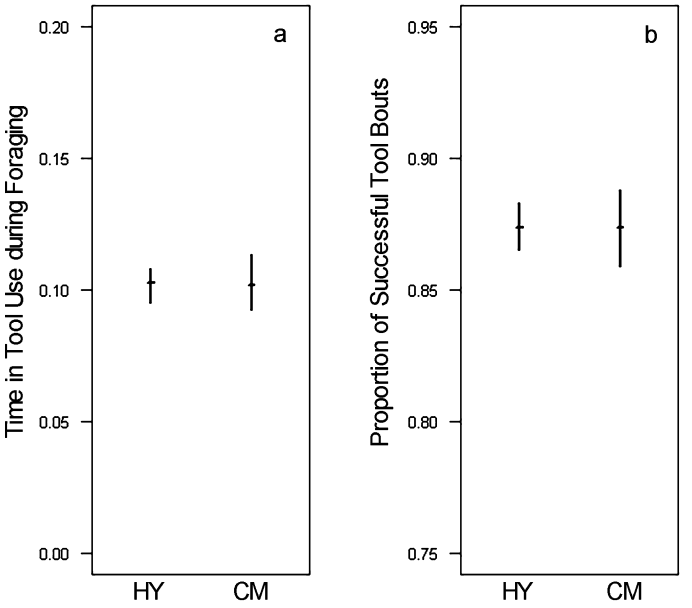


Figure 5. An analysis of the hybrid longtails (HY, CM) on Koram Island showed that performance of tool behaviour did not vary across phenotype. Test 2 showed the proportion of time spent in tool use during foraging (a) and Test 3 showed the proportion of successful tool bouts out of all bouts (b) were similar in both samples. Bars represent 95% confidence intervals.

2.437, SD = 0.979, $\chi^2 = 8.20$, df = 1, $p = 0.004$), while proximity to HY macaques was not found to be significantly related to whether a subject was a tool user (E = 0.676, SD = 0.712, $\chi^2 = 0.949$, df = 1, $p = 0.330$) (Table 5). These results tend to reject the notion that a very simple, unbiased social learning mechanism based on social closeness could account for the difference in tool user prevalence across the two phenotypes.

3.5. Overall model significance for each test

Overall, the set of predictors significantly differed from the null model in three of the four tests (Test 1: $\text{LRT}_{\text{Full vs. Null}}$: $\chi^2 = 14.898$, df = 4, $p = 0.005$; Test 2: $\text{LRT}_{\text{Full vs. Null}}$: $\chi^2 = 151.740$, df = 6, $p < 0.001$, and Test 4: $\text{LRT}_{\text{Full vs. Null}}$: $\chi^2 = 10.126$, df = 4, $p = 0.038$). In the full and null models of Test 3 significance at the $p < 0.05$ was not achieved. It did, however, reveal a clear trend ($\text{LRT}_{\text{Full vs. Null}}$: $\chi^2 = 7.12$, df = 3, $p = 0.068$), which was considered a result that could be evaluated (Stoehr, 1999).

Table 5.
Test 4: Differences between the two hybrid longtail phenotypes (HY, CM) in prevalence of tool users, after including social proximity with the hybrid phenotype (HY) to control whether the phenotypic difference in tool user prevalence was better accounted for by phenotypic biases in social association (full vs null $\chi^2 = 10.126$, $n = 38$, df $= 4$, $P = 0.038$).

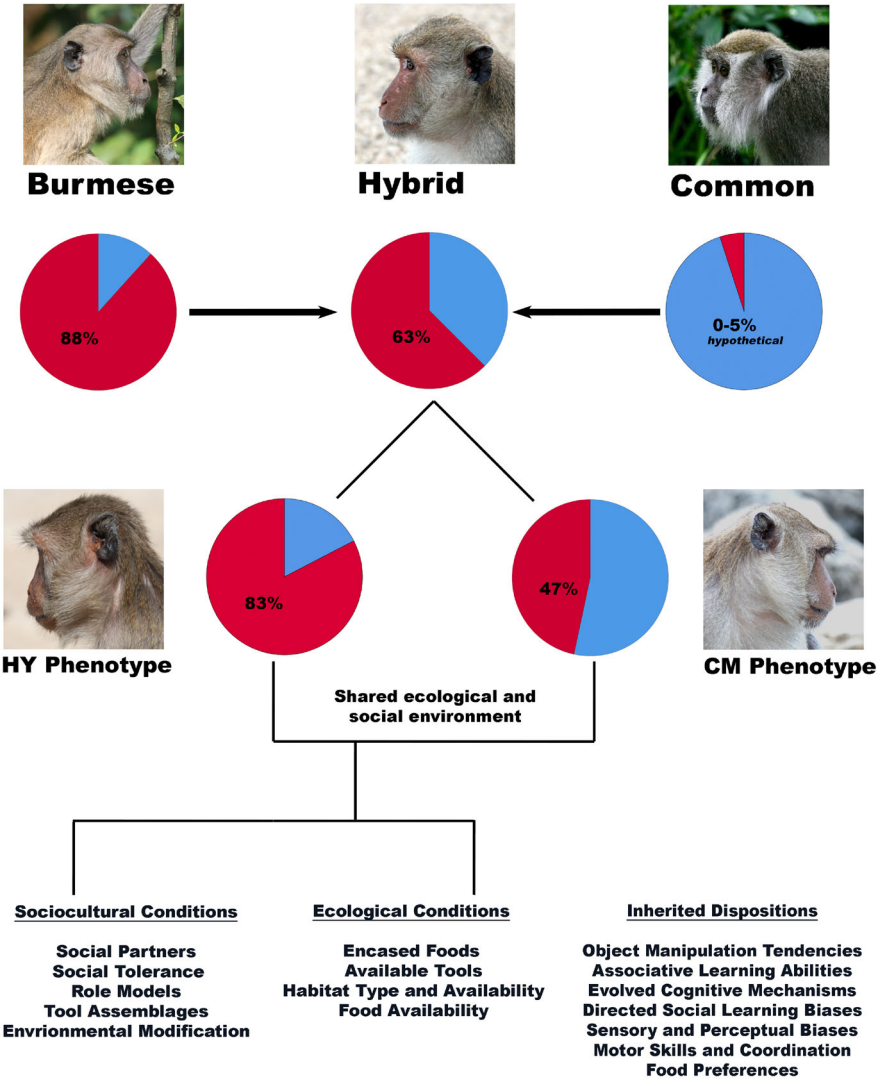
	Estimate	SE	df	χ^2	P
(Intercept)	−1.824	1.123	[a]	[a]	[a]
Tool user prevalence, HY & CM	2.437	0.979	1	8.200	0.004
Time in proximity to HY	0.676	0.712	1	0.949	0.330
Age (adolescent)[b]	0.478	1.139	1	0.181	0.671
Sex (male)	2.670	1.608	1	3.344	0.067

[a] Not shown because does not have meaningful interpretation.
[b] Ages used were adolescent and adult, both of mature tool user age.

4. Discussion

Test 1 showed that, in hybrid long-tailed macaques, facial hair pelage patterns that were indicative of parent subspecies type were statistically associated to whether an individual was a tool user or not. A sample of pure Burmese longtails at Laem Son National Park showed a higher prevalence of tool-using individuals compared to a sample of hybrid longtails (Figure 6). Amongst the hybrid longtail subjects, hybrid-like facial pelage phenotypes (HY) demonstrated a significantly greater prevalence of tool users than common-like phenotypes (CM). Results showed CM subjects expressed a significantly lower prevalence of tool users compared to the pure Burmese longtails (BM), while HY subjects did not. This pattern of results indicates that the lower proportion of tool users in the hybrid longtail sample, relative to the pure Burmese longtail sample, can be primarily accounted for by the lower tool user prevalence found within the CM sample. The power of this hybrid approach is that both the CM and HY phenotypes shared the same basic ecological and social environments, and thus the results are more consistent with inherited differences accounting for the variation found in the two phenotypes.

Although the two phenotypes in hybrid longtails differed in prevalence of tool users, Test 2 and Test 3 did not uncover any difference between phenotypes in two basic characteristics of tool behaviour — rate of performance and success in opening food. The CM individuals that were tool users, used tools just as often and proficiently as the HY tool users. Variation in the



Possible mechanisms underlying stone-hammering behavior

degree of tool user performance and skill across phenotypes was expected; however, not finding it does not obviate the difference found for prevalence in Test 1. Rather, it may help indicate where the difference between the phenotypes might lie, as it seems to show the motor capacity and coordination might be similar. What does seem to differ though is the probability of becoming a mature tool user, as measured in the proportion of mature tool users in each phenotype. Developmental biases could account for this difference.

The sample was drawn from a hybridized population of Burmese and common longtails, and thus the phenotypic discrimination does not separate them into their respective subspecies per se. Rather, each subject just resembles, more or less, either one of the two parent subspecies. The degree that each subject shares a genetic make-up with either parent subspecies is not known. Therefore, it is possible that the tool-using CM subjects may have had adequate Burmese introgression to be endowed with any biases for developing tool use. Since the CM tool users might still be affected by a Burmese ancestry, the results do not indicate that common longtails can acquire stone-hammering behaviour. That would have to be indicated in pure common longtail populations.

To date, there is still no evidence that pure common longtails anywhere have evolved stone hammering as a foraging strategy. Finding common longtails that engage in similar levels of stone hammering, across a similarly wide range, would overturn this conclusion. Taking what is known, however, from these results and other work, it seems that tool-assisted mollusc predation is a specific characteristic of the Burmese subspecies, and more specifically to those occurring in the Andaman Sea region around the Tenasserim Hills. Surveys of Burmese longtails in the northern parts of Myanmar lack reports of

Figure 6. A schematic diagram showing tool user potential across types and listing possible mechanisms underlying the development of stone-hammering behavior. Using the tool user prevalence values, the potential for developing into a mature tool user is shown in the pie charts next to each subspecies' variety — Burmese, common, and hybrid longtails. Common longtails were assigned a hypothetical value between 0–5%, since no cases of customary tool behavior exist, but they stone handle and use tools in a few places. The assigned value reflects that it is possible, but of low likelihood, for them to acquire stone-hammering behavior. The hybrid longtails are separated into their two facial pelage phenotypes and their prevalence scores. Some possible mechanisms supporting stone-hammering behavior are listed and categorized by ecological, sociocultural, and biologically-inherited factors. Brackets highlight that the two phenotypes studied shared ecological and social environments, but that their pelage differences could indicate they have inherited variations. The study here cannot discriminate across these mechanisms.

tool use (San & Hamada, 2011; Gumert et al., 2016), forcing consideration that this behaviour may not cover their entire range. The results, however, supporting the "absence of evidence" for tool behaviour in northern Myanmar are extremely scant, and firm conclusions cannot be drawn at this point.

Test 4 was used to rule out if a passive, non-specific social learning mechanism shared by both phenotypes could account for the phenotypic difference in behaviour observed. That is, a general ability to learn whatever one's regular nearest neighbours were doing. To measure this, proximity to social partners was used as the general measure of social association between individuals. If the difference between phenotype was the result of tool users simply being in close proximity to the more prevalent tool-using type, the HY phenotype, then it would not require any specialized learning abilities to cause the difference across phenotype. Test 4 could not reveal any evidence of a simple proximity-based mechanism being in operation here, and the phenotype-based difference remained significant. This finding did not support that non-specific social learning from nearest neighbours could alone account for the phenotypic difference observed in tool behaviour. Something more is required, and that could be directed developmental biases for acquiring stone-hammering behaviour that are associated with Burmese inheritance.

That stone-hammering behaviour may be inherently connected to one variety of macaque is a promising result, albeit an initial result based on a rapid assessment of pelage phenotype marking subspecies association. Taking what has been observed, signals this could be a model organism where a new hybrid method can be applied to help unravel the complex web of biological, ecological and sociocultural factors affecting development of customary tool-use behaviour in an intelligent primate (Figure 6). This could prove enlightening to the science of animal cultures. Particularly so for primates studies, which generally leave inherited factors much less discussed than cultural mechanisms. This is not to downplay or disregard cultural mechanisms affecting primate tool behaviour, nor do these current results suggest that macaque tool behaviour is genetically-fixed. They do, however, highlight a real possibility for important inherited influences on tool behaviour, in addition to factors already know to affect primate tool behaviour. How inherited factors interact with the better understood social and environmental processes that typically affect primate tool use will now need to be resolved. Possible mechanisms will be discussed below, but first the justification of the phenotype marker used will be addressed.

4.1. Justification of facial pelage subspecies marker

It could be argued that the thesis presented here is weak, due to using only pelage characteristics to discriminate phenotypic type. However, the morphological measure used to assign phenotype was shown previously to reliably discriminate Burmese and common longtails. Studies across Southeast Asia demonstrated clearly how facial pelage pattern, especially the lateral cheek crest, was distinctly different between samples collected from the *M. f. aurea* and *M. f. fascicularis* ranges (Fooden, 1995). Other morphological features also were found that exhibited variation; however, these had too much overlapping variation to discretely mark parent type (Fooden, 1995; Bunlungsup et al., 2016). Using unreliable measures like that would only produce irregular data and less definitive results, and also at a much higher cost in terms of time and use of animals. For example, in hybrid baboons in captivity, using a variety of morphometric measures that require capture and physical measurements showed too much phenotypic variation to discretely type them (Ackermann et al., 2006). Here though, in this study, a distinct and reliable morphological marker of parent type was easily scored from observations, without invasive capturing of wild animals, and allowed for quick assessment.

Qualitative marker traits can indicate hybridization more clearly, at least in the early stages of hybridization. For example, distinct qualitative features, such as head pelage, were found to be most reliably associated with behavioural differences in hybrid baboons, when compared to other markers of type (Bergman et al., 2008). The researchers finding this suggested it occurred because the morphological qualities marked relevant genetic differentiation better than other measures, including genetic fingerprinting, as it only targets small, unassociated portions of the genome (Bergman et al., 2008). The argument they presented over morphological vs. genetic measures of pedigree is noteworthy and a discussion in itself. In the case here, it does offer some validation to the use of a qualitative morphological marker to assign closeness to parent type in hybrid animals. Furthermore, it makes the key point that applying incomplete genetic analysis could actually be more confusing, than clarifying. Lastly, several other studies show pelage pattern to be a good indicator of hybridization, being used to discriminate hybrids in rhesus (*M. mulatta*) and long-tailed macaques (Hamada et al., 2016), wild Scottish (*Felis silvestris grampia*) and domestic cats (*F. catus*) (Beaumont et al., 2001), *Alouatta pigra* × *A. palliata* howler monkeys (Kelaita

& Cortés-Ortiz, 2013) and *Alouatta guariba* × *A. caraya* howler monkeys (Cortés-Ortiz et al., 2015). Taken together, pelage pattern can be a useful tool for discriminating type in behavioural field studies of hybrids.

The pelage pattern of the lateral facial crest in macaques is the only known diagnostic feature for discriminating Burmese and common longtails. Fooden (1995) showed that an infrazygomatic pattern (IZ) of the lateral facial crest was found in Burmese longtails, while a transzygomatic pattern (TZ) was found in common longtails (Figure 2). This was very reliable, as indicated in his data. Amongst 819 full-body pelage specimens collected across Southeast Asia, 83 showed IZ. There were 51 IZ patterns found in Bangladesh and Myanmar, all within the range of *M. f. aurea*, while zero cases of TZ were found in the same region. Another 16 of the 83 IZ patterns were found in the longtail hybrid zone (Figure 1) where there was TZ–IZ variation across individuals, and eight of those showed mixed-pelage patterns within an individual (i.e., one side of face IZ, one side TZ). Nine more IZ patterns were found along the northern border of the common longtail range where they hybridized with rhesus macaques (*M. mulatta*), a species that also exhibits IZ lateral crests.

An additional 15 IZ patterns were found outside the core and hybrid ranges. Three were in the Nicobar Islands, and ten on Simeulue and Lasia Islands, west of northern Sumatra. All of these islands have endemic long-tailed macaques subspecies, *M. f. umbrosa*, *M. f. simeulue*, and *M. f. lasiae*, respectively. All showed mixed lateral crest patterns, similar to the hybrid longtail zone. These islands, in the past, were likely larger land masses with some interconnections during lower sea level periods around 125 000 years ago. As such, the pelage pattern mixing along this Nicobar-Andaman Ridge could be related to the modern subspecies around the Andaman having had some historical contact. Global sea level variability, however, has not exceeded 250 m in the last 50 million years (Miller et al., 2005) and bathymetry shows these islands were unlikely ever fully connected (Curray, 2005). Contact, therefore, would have required passing these deeper regions, and thus is an uncertain scenario. The two most anomalous IZ patterns were found in the common longtail range in Bintan and Kalimantan, bearing no connection to this Andaman region. The reason for the two anomalies is unknown, but overall, an infrazygomatic lateral crest is a distinctive feature always found in the Burmese subspecies, occurs in hybrids, and is ostensibly absent in common longtails.

4.2. Mechanisms underlying variation in tool behaviour

Tool behaviour in macaques should be affected by an interaction of ecological, sociocultural, and inherited factors (Figure 6). In this study, tool behaviour did not seem to equally transfer to all individuals in a hybrid population, which is not what is expected if there is a general species-wide ability in long-tailed macaques to develop stone-hammering behaviour. By contrast, it supports the alternative hypothesis that there could be more ultimate, inherited biases accounting for the phenotypic difference. Across the hybrid longtail phenotypes (HY and CM), the social and ecological conditions were largely shared; however, inherited traits might not be as closely shared, as indicated by the phenotypic variation in pelage patterns and tool behaviour. Tool behaviour was more strongly related to the pelage marker of Burmese longtail ancestry. This is consistent with Burmese longtails having inherited biases towards developing stone-hammering behaviour. Possible mechanisms affecting stone-hammering behaviour are discussed below, examining environmental features and inherited factors.

4.3. Ecological influences on tool behaviour

Long-tailed macaque stone-hammering behaviour has an obvious ecological linkage. It is highly specific to coastal environments with abundant rocks and molluscs. Long-tailed macaques also will move in from coasts and crack nuts inside coastal forests (Gumert et al., 2009; Falótico et al., 2017; Luncz et al., 2017a); however, there are no known examples where stone-hammering longtails are disconnected from coastal habitats. Given this tight link to habitat, the difference between Burmese and common longtails in tool behaviour could have been simply that Burmese longtails live on coasts, and common longtails do not. Although a sound hypothesis, the results found in this study go against this notion, as they cannot account for why two phenotypic classes of individuals living in the same ecological conditions would vary in their prevalence of tool behaviour. The results found though are in accords with an experiment (Bandini & Tennie, 2018) and surveys through the longtail range showing a lacking tool ability in common longtails. Common long-tailed macaques live in numerous environments all over Southeast Asia (Gumert et al., 2011), including coastal habitats with similar ecologies to their Burmese counterparts. At these coastal sites, however, behavioural and artefactual evidence of stone-hammering behaviour is strikingly absent (Gumert et al., 2014, 2016). There currently is no evidence that given the

right proximate ecological conditions, pure common longtails will develop stone hammering, as Burmese longtails do.

On the other hand, how pervasively the ecological conditions affect either subspecies, could produce differing degrees of natural selection on the two subspecies. That is, ecology could be playing a key role in the evolution of developmental biases supporting the behavioural divergence between these two subspecies. Tool-using Burmese longtails inhabit the region around the Tenasserim Hills, Isthmus of Kra, and the numerous islands of the Mergui Archipelago. In this region, landmass is severely limited, and insular, coastal, and estuarine habitats compose a very large proportion of the population's range. These conditions seem suitable for capacities underlying stone hammering to be selected for through natural selection, since much of the population would be affected by the ecological challenges of foraging for their nutritional needs in flooded habitats (Gumert et al., 2019). The Burmese population, around the Mergui Archipelago, overlaps coastal habitats more so than the common longtail population in general. No evidence to date shows that common longtails quickly pick up this behaviour when exposed to the appropriate ecological conditions. Evolutionary changes, however, may have differentiated the subspecies inherent tool-use abilities, an thus Burmese and common longtails do not share an inherited equipotential to proximately respond to coastal habitats by adopting stone hammering. The results in the hybrid study are quite consistent with this hypothesis; however what those biases could be were not uncovered. Possibilities are discussed below.

4.4. Social environment and tool behaviour

The social environment can have a supportive effect on the development of tool behaviour. This can be presence and access to social partners who serve as role models, and how their activities construct the environment. For example, gregariousness and social tolerance were shown to be important aspects in the transmission of behaviour learned through social processes (van Schaik, 2003; Lind & Lindenfors, 2010). Thus the number of social partners in a group, particularly females, and how tolerant partners are towards each other can foster a greater likelihood for cultural traits to persist. There are no studies on the social behaviour of Burmese longtails, but at the species-level long-tailed macaques are generally not considered very tolerant, although they are gregarious (Thierry, 2000). Also important is the impact that social partners have on the environment by leaving artefacts relevant to tool

behaviour (Laland et al., 2000; Carvalho et al., 2009; Fragaszy et al., 2013; Tan, 2017). In this study, both phenotypes shared the same basic social environment and thus had similar exposure to these types of factors. What could have differed though, was inherited biases directed towards these features. For example, each phenotype might have varied in their social interest or tolerance towards others. Test 4's results, however, are not really congruent with there being any differences in social association affecting tool behaviour variation across type. Another possibility is that each phenotype varied in their motivation to interact with artefacts and debris left at tool assemblages during development.

4.5. Object manipulation and tool behaviour

The inclination to manipulate objects found in the environment is one possible difference that could affect the Burmese longtails' potential for developing stone-hammering behaviour. Young Burmese longtails do regularly manipulate stones and shellfish, thus this tendency is involved in the development of stone-hammering behaviour (Tan, 2017). In general, macaques have well-formed hands and a high manipulative potential (Liu et al., 2016), thus showing important key features that could support stone-hammering behaviour and other forms of tool use. Congruent with this ability, are that several macaque species, including longtails, exhibit playful stone handling in temples and captivity that serves no foraging function (Huffman, 1984; Huffman & Quiatt, 1986; Leca et al., 2007; Nahallage & Huffman, 2008, 2012; Pelletier et al., 2017). Stone handling gives the impression that macaques have an underlying disposition supportive of tool behaviour and that it just needs the right conditions to canalize into functional tool use. If true, tool-use behaviour should arise commonly in macaques; however, it does not.

Macaques are not generally considered talented tool users (Panger, 2007; Macellini et al., 2012), which contradicts that they have a potential for tool behaviour from their high manual dexterity and propensity to play with objects. Perhaps then, macaques fall just short in the necessary requisites to be prolific tool users. Maybe they are just not quite manipulative enough, cannot associate the objects to foraging, or some other relevant lacking capacities. Burmese longtails, on the other hand, may have stepped over that fine line, due to the conditions of their evolution, showing once unleashed, macaque motor abilities can derive highly frequent and skilled tool behaviour. The rock and mollusc rich coastal habitats affecting much of the Burmese subspecies' in the Tenasserim region, could have been that selective pressure.

Observations of pet Burmese long-tailed macaques give the impression they are prolific object manipulators, showing stick use, stone throwing, body manipulations, stone handling, and stone hammering (Gumert, personal observations during 2008–2016). There are, however, no comparative studies of their object manipulation capacities in controlled settings, thus such a difference remains only an impression.

The importance of object manipulation to tool behaviour is obvious in other tool-using primates. For example, capuchins are extremely manipulative of objects, naturally pounding food items onto hard surfaces and showing prerequisite abilities for easily developing tool use (Fragaszy & Adams-Curtis, 1991; de Resende et al., 2008). Similarly, chimpanzees (*Pan troglodytes*) show a high intrinsic motivation towards manipulating objects and using tools, and these tendencies were shown to be higher than in bonobos (*P. paniscus*) (Koops et al., 2015). This finding is important because in the wild, bonobos hardly use tools, while chimpanzees have the most complex tool behaviour of all animals (Furuichi et al., 2015). What Koop's et al. study uncovers is that just minor differences in object manipulation biases, could potentially have profound effects on the extent of tool use and material culture an animal develops in the wild. Could similar biases be contributing to the difference in tool behaviour between Burmese longtails and other macaques?

4.6. Learning tool-use behaviour

Tool use generally requires some exploration and learning from the surrounding environment, and this can involve both social and asocial processes. The role of social learning in development of tool behaviour is strongly emphasized, especially in primate studies (Fragaszy & Adams-Curtis, 1991; Coussi-Korbel & Fragaszy, 1995; Whiten et al., 1999, 2017; Whiten, 2000; Laland, 2001, 2004; Fragaszy & Visalberghi, 2004). Asocial learning, on the other hand, is also important to the development of tool-use behaviour (Kenward et al., 2005; Macellini et al., 2012); however, individual-level associative learning is less often discussed in regards to animal tool behaviour (Lind, 2018). A full discussion of learning and tool behaviour is beyond the scope of this discussion, but the point to be made here is that individual-level biases can influence both social and asocial learning abilities, and thus could potentially vary across the macaque subspecies being considered here.

That asocial learning abilities can vary is pretty straightforward and associated with intelligence. For social learning, however, it does not necessarily

require the individual to have strong associative learning abilities. That is, they could just have very simple mechanisms to copy those with whom they have the most social association, resulting from a docile disposition to learn from others (Simon, 1990), rather than really generating, or innovating, their own learned associations between objects and their uses. Test 4 ruled out this simple type of social learning mechanism as being able to account for differences in tool user prevalence across phenotype, but still leaves open the possibility of more directed learning biases and evolved cognitive mechanisms affecting learning abilities (Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 2004; Laland, 2004; Lotem et al., 2017). Learning is not a passive response to the environmental conditions, but requires internal dispositions and developmental biases to operate. In this regard, Burmese longtails could differ from common longtails and other macaques.

In hybrid longtails, there is a long learning process that occurs during a young macaques development. This involves both social and asocial learning processes. Attentional biases in young macaques have been observed that are more than just biases for closest associates, and are directed towards older and more skilled tool user models (Tan et al., 2018). Tool behaviour acquisition also involves young macaques directing interest towards objects, resulting in independent and unstructured interactions with the relevant materials for stone-hammering behaviour. The proper association of the objects improves over time (Tan, 2017). This process shows how individual associative learning abilities are contributing to tool behaviour in longtails. Notably, across several macaques species, nearly all cases of tool use studied in captivity showed larger contributions of asocial learning for acquiring tool behaviour, than social processes (Anderson, 1985; Zuberbühler et al., 1996; Ducoing & Thierry, 2005; Macellini et al., 2012). These findings could apply to wild macaque tool behaviour as well. Macaque stone-hammering behaviour is likely being operated on by both social and asocial learning mechanisms when they are young, which could be supported by developmental biases and learning potentials.

4.7. Integrative models of learning

One of the best integrative models of learning has been formulated from classic studies on sparrows, which identified learning features that were referred to as "instincts to learn" (Marler & Tamura, 1964; Marler & Peters, 1977; Marler, 1991, 2004). In a series of studies comparing song sparrows

(*Melospiza melodia*) and swamp sparrows (*M. georgiana*), it was found each species more easily learned elements of their own species' songs when experimentally exposed to the songs of both species during development. That is, when given choices, the sparrows did not arbitrarily learn whatever social information was passively present in the environment. Rather, they demonstrated inherent developmental biases to attend to specific vocal components of song over others. The findings did not support an equipotential between the two sparrows in learning any song pattern, but instead that each species was internally predisposed to specific types of information. These studies illustrate quite nicely how closely related taxa can have distinct learning biases that integrate a variety of factors into the process of learning behaviour.

More specific to tool use, when given sticks in an experimental task, New Caledonian crows (*Corvus moneduloides*) show they can learn tool use in the absence of any social models (Kenward et al., 2005). This shows an intrinsic bias to develop stick tool use when relevant environmental components are present. In this experimental setting, their tool behaviour developed entirely in the absence of social influence; however, field studies present a more integrative picture. Social learning has also been shown to contribute to development of tool use and manufacture, illustrating a complex scenario of integrated factors affecting tool behaviour development. On top of their individual-level proclivity to acquire tool behaviour, cultural differences were observable amongst wild populations, and tool development was shown to be improved by observing skilled social role models (Hunt & Gray, 2003; Hunt et al., 2007; Holzhaider et al., 2010a,b).

The cases of sparrows and crows illustrate nicely how learned animal behaviour is affected by an interdependency of factors in the environment and inherited developmental biases. An inherited disposition can be "prepared" for certain environmental elements, such as type of song or material, with "proper" development occurring when those inherited dispositions can interact with the appropriate environmental features. Such adaptive behaviour cannot fully develop unless it has the correct integration of the necessary environmental and inherited components. That is, the learning mechanisms are adapted to reliable features of the environment, factors that Marler called "instincts to learn". This phenomenon could be referred to as a specialized learning capacity, an evolved psychological or cognitive mechanism, or a directed learning strategy. Burmese longtails might have something like this supporting their stone-hammering behaviour. Future work can further consider these possibilities.

4.8. Are Burmese longtails specialized learners?

There appears to be a uniqueness about Burmese long-tailed macaque stone-hammering behaviour when compared to other long-tailed macaques, or really to all Old World monkeys. Remaining within the species though for comparative purposes, there are occasional reports of tool behaviour observed here and there in other longtail subspecies, common longtails (Chiang, 1967; Wheatley, 1988, 1999; Fuentes et al., 2005; Watanabe et al., 2007) and Nicobar longtails (*M. f. umbrosa*) (Pal et al., 2017). None of these cases, however, compare in extent to Burmese longtails. For example, tool behaviour in Nicobar (Pal et al., 2017) and Burmese longtails distinctly differ in their type and frequency. In Nicobar longtails, 56 cases of leaf rubbing and 25 cases of tooth-flossing (total = 81) were reported during 1660 h of observation. In contrast, Burmese longtails used stone tools much more frequently, as in 11 h of group observation, 2449 stone-tool bouts were recorded (Haslam et al., 2016). In hybrid longtails too, about 7400 tool bouts were observed during 499 h of individual focal observation (Tan, 2017). The numbers here are enormously different, begging the question why. What is different about Burmese longtails?

The difference seems best accounted for by a special capacity underlying stone-hammering behaviour in Burmese long-tailed macaques. If this were not the case, it would be expected that functional stone hammering, or other forms of tool behaviour, should be more widely distributed amongst macaques, and occur in similar frequencies where it is found. There is, however, no evidence anywhere even suggesting this is true. Rather, macaque tool behaviour of this magnitude is currently only found in one subspecies, in one region, for one mode of foraging, around one kind of environment. Current evidence makes it reasonable to consider that Burmese long-tailed macaque stone-hammering behaviour is a specialized learned trait, adapted to specific ecological conditions shared by much of their population, and now has underlying developmental biases supporting its reliable acquisition. The association of stone-hammering behaviour with Burmese long-tailed macaques was evidenced in this study by finding an association between tool behaviour and a reliable subspecies pelage marker. Hybrid longtails provide a new approach for testing the integration of ecological, sociocultural, and inherited influences on animal tool behaviour. Genetic research is the obvious next step here, which potentially could uncover genetic or epi-genetic systems associated with inherited dispositions affecting behaviour.

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